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Cover crops enhance soil organic matter, carbon dynamics and microbiological function in a vineyard agroecosystem

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ABSTRACT

Impacts of soil tillage and cover crops on soil carbon (C) dynamics and microbiological function were investigated in a vineyard grown in California's mediterranean climate. We (1) compared soil organic matter (SOM), C dynamics and microbiological activity of two cover crops [Trios 102 (*Triticale* × *Triosecale*) ('Trios'), Merced Rye (*Secale cereale*) ('Rye')] with cultivation ('Cultivation') and (2) evaluated seasonal effects of soil temperature, water content, and precipitation on soil C dynamics (0–15 cm depth). From treatments established in November 2001, soils were sampled every 2–3 weeks from November 2005 to November 2006. Gravimetric water content (GWC) reflected winter and spring rainfall. Soil temperature did not differ among treatments, reflecting typical seasonal patterns. Few differences in C dynamics between cover crops existed, but microbial biomass C (MBC), dissolved organic C (DOC), and carbon dioxide (CO_2) efflux in 'Trios' and 'Rye' were consistently 1.5–4-fold greater than 'Cultivation'. Cover crops were more effective at adding soil C than 'Cultivation'. Seasonal patterns in DOC, and CO_2 efflux reflected changes in soil water content, but MBC displayed no temporal response. Decreases in DOC and potential microbial respiration ($RESP_{mic}$) (i.e., microbially available C) also corresponded to or were preceded by increases in CO_2 efflux, suggesting that DOC provided C for microbial respiration. Despite similar MBC, DOC, $RESP_{mic}$, annual CO_2 efflux and aboveground C content between the two cover crops, greater aboveground net primary productivity and SOM in 'Trios' indicated that 'Trios' provided more soil C than 'Rye'.

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1. Introduction

Cover crops provide many services to agroecosystems. In particular, they decrease erosion, improve infiltration and reduce runoff, improve soil nutrient retention, and build soil organic matter (SOM) (Battany and Grismer, 2000; Jackson, 2000). Cultivation, a common practice in agroecosystems, has been linked to reductions in SOM, which occurs by oxidation of SOM protected within soil aggregates prior to tillage, and causes short-term perturbations in soil microbial biomass and activity (Six et al., 1999; Calderón et al., 2000, 2001). No-till and minimum tillage practices have become increasingly popular as a means to reduce SOM loss. Much of the research on the influence of cover cropping, no-till, and reduced tillage practices on SOM has occurred in temperate regions (e.g., Six et al., 1999; Grandy and Robertson, 2007; Hermle et al., 2008), but recent findings suggest that combining cover crops with no-till practices and shifting tillage intensity may similarly enhance ephemeral and longer-term pools of SOM in Mediterranean and semiarid annual agroecosystems (Andrews et al., 2002; Hulugalle et al., 2006; Veenstra et al., 2007; Álvaro-Fuentes et al., 2008).

Mediterranean climates are characterized by cool, moist winters, which involve frequent wet–dry cycles, and dry,

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warm summers. In Mediterranean ecosystems, soil carbon dioxide (CO_2) efflux and microbial biomass carbon (MBC) have distinct seasonal dynamics, and in particular, portray strong increases after simulated rainfall (Lundquist et al., 1999a,b; Fierer and Schimel, 2002; Steenwerth et al., 2005). These studies have occurred in many Mediterranean ecosystems, including cole crops, tomatoes, annual and perennial grasslands, and oak woodlands (Lundquist et al., 1999a,b; Casals et al., 2000; Fierer and Schimel, 2002; Rey et al., 2002; Maestre and Cortina, 2003; Steenwerth et al., 2005). However, little information on the impacts of cover cropping and cultivation on soil respiration (i.e., root + microbial respiration), MBC, dissolved organic carbon (DOC), and other labile C pools presently exist for perennial agroecosystems (Carlisle et al., 2006). Perennial agroecosystems may support different soil carbon (C) dynamics than annual agroecosystems due to the lower frequency of soil disturbance by tillage.

Vineyards represent an ideal perennial agroecosystem in which to utilize cover crops and no-till practices to enhance SOM content and soil microbiological function. Cover crops grown in the alleys between grapevines are planted after minor soil preparation, with physical soil disturbance occurring as little as once per year. This is comparatively less frequent than in annual agroecosystems, which annually can support two to four crop rotations and experience multiple tillage passes. In the U.S. alone, grape-bearing acreage covered approximately 1.4 million ha in 2005, and vineyards now exist in every state, although 77% of all vineyard land use is in California (USDA/NASS). In California, the most recent documented estimates indicate that only approximately 16% of vineyards supported cover crops (Ingels and Klonsky, 1998). Vineyard cover crops are typically planted in the fall at the onset of precipitation (ca. October to November), receive no irrigation, and grow throughout the rainy season into late spring (ca. March to April) while the grapevines are dormant. Typically, they are mowed or tilled near spring budbreak to decrease potential frost damage to the grapevines. Given the benefits of cover cropping in other agroecosystems and the large spatial extent of vineyards, demonstrating potential benefits of cover cropping on soil C pools and microbiological function in vineyards has high potential for practical impact and adoption.

In order to understand how cover crops and cultivation affect soil C dynamics in a vineyard, we established our study in a Chardonnay vineyard in the Central Coast (Monterey Co., CA), a region with one of the largest contiguous stretches of vineyards in the world. The cover crop and cultivation treatments in the vineyard floor had been established 4 years previously as part of another study (Baumgartner et al., 2005). The cover crops, Trios 102 (*Triticale* × *Triosecale*) and Merced Rye (*Secale cereale*), had been selected due to their contrasting aboveground growth patterns. Typically, Trios 102 has less aboveground biomass and a more prostrate growth form relative to Merced Rye (*S. cereale*) early in the growth season. Trios 102 bolts later than Merced Rye, but they are nearly indistinguishable in morphology and aboveground by the end of the growth season in late spring just prior to mowing or tilling. In the present study, we (1) compared effects of cover crops and cultivation on soil C dynamics, CO_2 efflux, soil microbiological activity, and SOM content, (2) evaluated seasonal effects of soil temperature, water content, and precipitation on soil C dynamics, and (3) determined potential drivers of CO_2 efflux in this vineyard agroecosystem.

2. Materials and methods

2.1. Site description and experimental design

This study was conducted in a vineyard in the Central Coast region of California (Greenfield, Monterey County, CA). The vineyard was established in 1996 with *Vitis vinifera* L. cv. Chardonnay on Teleki 5C (*V. berlandieri* Planch. × *V. riparia* Michx.) rootstock. Vine spacing was 2.4 m between rows and 1.8 m within rows. Since establishment, the alleys were planted with barley (*Hordeum vulgare*) (112 kg ha^{-1}) every fourth year. Barley was allowed to set seed prior to mowing to promote self-reseeding. Every other year, the soil was ripped with two steel shanks to 71–76 cm depth, followed by two passes using a tandem disc and roller prior to seeding.

As part of another study, three treatments were established in the alleys in 2001 (Baumgartner et al., 2005). These treatments included two cover crops, Trios 102 (*Triticale* × *Triosecale*) and Merced Rye (*S. cereale*), and a cultivated treatment. Hereafter, these will be referred to as 'Trios', 'Rye', and 'Cultivation', respectively. The experimental design for the current study was a randomized complete block, with row serving as block. Grapevine rows in this vineyard measured 506 m long, and were oriented west to east. Within each of three blocks, treatment plots each consisted of 1/6 of the row length (84.3 m), in the alleys between two rows of grapevines. There were two replicates of each treatment (i.e., 'Rye', 'Trios', and 'Cultivation') per block ($n = 6$ replicates per treatment). During this study, the soil was not ripped with steel shanks. Cover crops were sown (112 kg ha^{-1}) into the center 1.8 m of the 2.4 m between row space (alley) using a Tye grain drill with disc openers. 'Rye' and 'Trios' were mowed using a 106 cm wide flail mower in mid-April, leaving cover crop residue on the vineyard floor. 'Cultivation' was tilled approximately once every 2 months using a tandem disc and ring roller, as necessary for weed control, and visual estimates indicated that weed cover did not exceed more than 10% cover.

The current study was initiated during the fifth and final year of the original study, beginning with cover crop planting in November 2005 and continued until November 2006, coinciding with one season of cover crop and grapevine growth. Table 1 outlines the timetable of vineyard floor management practices and sampling dates. Soil and plant samples (except for root samples) were collected every 2–3 weeks from random locations within each treatment replicate for a total of 19 sampling dates.

Soil type was the Elder loam series (coarse–loamy, mixed, superactive, thermic Cumulic Haploxeroll) (Cook, 1978). The composition of sand, silt, and clay was 62.2 ± 0.3%, 23.3 ± 0.3%, and 14.6 ± 0.2%, respectively ($n = 18$). Other soil characteristics in the 0–15 cm layer were: 15.27 ± 0.14 cmol CEC kg^{-1}, 0.17 ± 0.07 cmol exchangeable (X–)Ca kg^{-1}, 0.28 ± 0.02 cmol X–Na kg^{-1}, 3.13 ± 0.04 cmol X–Mg kg^{-1}, 0.76 ± 0.06 cmol X–K kg^{-1}, 1, and pH of 7.19 ± 0.04 ($n = 18$).

Table 1 – Timetable of vineyard floor management events, biweekly sampling dates, and management and precipitation events, and corresponding dates used to test *a priori* hypotheses

Season	Date	Biweekly sampling (BS) or vineyard floor management practice[a]	Events compared through multiple comparison	Sample dates compared through multiple comparisons[b]
Winter	20 November 2005	'Cultivation' tilled; 'Rye' and 'Trios' tilled and planted		
	30 November	BS	'Winter rain'	30 November 2005 vs. 10 January 2006
	13 December	BS		
	10 January 2006	BS	'Winter dry-down'	10 January vs. 6 February
	24 January	BS		
	6 February	BS		
Spring	8 March	BS	'Spring rain'	6 February vs. 8 March
	21 March	BS		
	7 April	'Cultivation' tilled		
	13 April	BS	'Tillage'	21 March vs. 13 April
	20 April	'Rye' and 'Trios' mowed		
	26 April	BS	'Mowing'	13 April vs. 26 April
	9 May	BS		
	30 May	BS		
Summer	5 June	'Cultivation' tilled		
	12 June	BS		
	17 July	BS		
	8 August	BS		
	23 August	'Cultivation' tilled		
	30 August	BS		
Fall	19 September	BS	'Fall rain'	19 September vs. 10 October
	10 October	BS		
	24 October	BS		
	14 November	BS		

[a] Six date comparisons selected prior to analysis multiplied by three treatments gives 18 comparisons; Bonferronni adjusted significance level of $p = 0.05/18 < 0.003$.
[b] The three vineyard floor treatments were 'Rye', 'Trios', and 'Cultivation'. ''BS'' is an abbreviation for ''Biweekly Sampling''.

The climate in Greenfield is Mediterranean, with heavy winter rains and summer drought conditions. Average daily temperatures range from 8 °C in the winter to 19 °C in the summer, which were typical for the region; annual rainfall recorded at the vineyard site for during the period of study (November 2005 to November 2006) was 46.9 cm (D. Salm, personal communication). Annual precipitation typically decreases in amount as one travels from north to south in the Salinas Valley where Greenfield exists. At the nearest weather station approximately 20 km to the southeast, the 14-year mean annual precipitation was 32.0 ± 5.1 cm (#113, King City Station, California Irrigation Management Information System [CIMIS], www.cimis.water.ca.gov). This suggests that the precipitation in the vineyard during the year of study may have been slightly above average, but the pattern in rainfall was typical for a Mediterranean climate.

We divided the 12 months of sample collection into four seasons differentiated by precipitation, temperature, and cover crop growth patterns (Table 1). In this experiment, winter (November to February) was characterized by cool soil temperatures (6–12 °C), rainfall (8–16% GWC), and minimal cover crop seedling growth and relatively bare ground in 'cultivation' in the alleys. Spring (March to May) had warmer soil temperatures (9–19 °C), heavy rainfall (10–22% GWC), and steady cover crop growth until mowing in mid-April. Summer (June to August) was warm (soil temperature 20–30 °C) and dry (5–8% GWC) with cover crop residue on the soil surface in 'Trios' and 'Rye' and no plant growth in the alleys, except for a few deep-rooted annual weeds (ca. 5–10% cover) in 'Cultivation'. In fall (September to November; final sample collection on 14 November 2006), soils were warm but cooling (soil temperature 15–20 °C), with the first rainfall in early October (range of 4–9% GWC), and no plant growth in the alleys due to lack of rainfall. In summer and fall, plant biomass from the mowed cover crops provided ground cover in both 'Rye' and 'Trios'.

2.2. *Plant biomass and soil sampling*

Aboveground cover crop and weed biomasses were collected from randomly placed quadrats (1.0 m × 0.5 m; $n = 3$ per treatment replicate) in 'Rye' and 'Trios' approximately every 2 weeks from seedling emergence to mowing. Plant material was clipped at soil level, and weed and cover crop biomass was separated, dried at 60 °C for 48 h, and weighed. Aboveground net primary productivity (ANPP) was determined as the net increase in total plant aboveground biomass (Milner and Hughes, 1968). To investigate root and shoot biomass allocation between cover crops, root biomass was collected toward the end of the growing season while aboveground biomass differed between 'Trios' and 'Rye' (i.e., 8 March 2006). In each treatment replicate, three 'cubes' of soil from 0 to 10 and 10 to

20 cm (20 cm × 20 cm × 10 cm), respectively, were removed with a digging knife. Roots were gently washed in a series of sieves ranging in mesh size from 60 μm to 1 mm to remove soil particles while retaining roots. Roots were removed with tweezers and dried at 60 °C for 48 h, and weighed. Cover crop and weed roots were not separated, but roots were collected from areas with relatively fewer weeds for these samples only. Total C of aboveground cover crop and root material were determined by combustion (Pella, 1990).

In each treatment replicate, two subsamples of soil (0–15 cm depth) were collected randomly from 'Rye', 'Trios', and 'Cultivation' treatments and mixed (ca. 500 g sample). Soil samples were taken between 10 a.m. and 12 p.m., placed immediately on ice, and stored within 6–8 h of collection overnight at 20 °C. All laboratory analyses were conducted within 24–48 h of sample collection. Soil temperature (0–15 cm) was taken from each plot at the time of sampling with a Li-Cor LI-6400 (Li-Cor Biosciences, Lincoln, NE, USA).

Soil gravimetric water content (GWC) was measured by drying a subsample (ca. 30 g wet wt.) at 105 °C for 48 h. Soil MBC was determined by 0.5 M K_2SO_4 fumigation–extraction (25.00 ± 0.05 g wet wt.) (Brookes et al., 1985; Vance et al., 1987). DOC in the MBC extracts was measured on a Shimadzu TOC-V_{CSH} unit (Shimadzu Scientific Instruments, Columbia, MD, USA). MBC was calculated from the relationship: biomass $C = E_C/k_{EC}$ (E_C = [organic C extracted from fumigated soil] − [organic C extracted from non-fumigated soil]; $k_{EC} = 0.45$) (Wu et al., 1990; Joergensen, 1996). Potential microbial respiration ($RESP_{mic}$) was measured by placing soil (ca. 100 g wet wt.) adjusted to 40% water filled pore space (WFPS) in sealed jars (946 cm^3), and measuring the difference in headspace CO_2–C concentration after 24 h at 25 °C. $RESP_{mic}$ served as a measure of microbially available C. Headspace CO_2 levels were measured using an infrared CO_2 analyzer (model PIR-2000R; Horiba Instruments, Irvine, CA, USA). Total soil C content was measured by combustion (Pella, 1990).

2.3. Soil CO_2 efflux

To develop an estimate of annual soil C lost through soil respiration, soil CO_2 efflux was measured *in situ* using a nondispersive infrared gas analyzer with an attached soil respiration chamber (Model LI-6400/6400-09; LI-COR, Lincoln, NE). Soil CO_2 efflux was measured by fitting the soil respiration chamber to polyvinyl chloride (PVC) rings (5 cm depth × 10 cm diameter), which were placed in the alley of each treatment replicate at the beginning of the experiment and remained in place throughout sampling ($n = 6$ per treatment). The only exception to PVC ring permanency was in 'Cultivation', where rings were removed when plots were tilled and then replaced at least 24 h prior to sampling. PVC rings were protected by metal disking plates to during mowing, and these were removed just after mowing. In the cover crop treatments, PVC rings were placed within the matrix of plants, but were maintained without plants to reduce error from differences in volume within the gas sampling chamber. Collection of soil respiration measurements began approximately 2 h before solar noon.

2.4. Statistical analyses

Prior to analysis, transformations were made to normalize the data as follows: GWC, soil temperature, $RESP_{mic}$, and MBC with a square root transformation; weed biomass and CO_2 efflux with a $\log_{10}(x + 1)$ transformation; cover crop biomass, and DOC with a $\log_{10}(x)$ transformation. Root biomass, root and aboveground plant tissue percent C and soil percent C were untransformed.

Analysis of variance (ANOVA) was conducted using a mixed model for repeated measures analysis to determine effects of treatment, date and treatment–date interaction on response variables (Proc Mixed, SAS Version 8.2, SAS Institute, Cary, NC, USA). To model variable correlation across dates, the covariance structure used for cover crop biomass, weed biomass, GWC, soil temperature, and MBC was compound symmetry. The covariance structure used for DOC, $RESP_{mic}$, and CO_2 efflux was auto regressive one. Covariance structures were chosen based on the Akaike information criterion (AIC). Effects of treatment for root biomass, plant percent C, soil percent C, and total annual CO_2 efflux were determined by a general linear model (Proc GLM, SAS Version 8.2, SAS Institute, Cary, NC, USA). Multiple linear regressions of CO_2 efflux on GWC, soil temperature, DOC, MBC, and $RESP_{mic}$, and MBC on GWC, soil temperature, $RESP_{mic}$, and DOC were also conducted (Proc REG, SAS Version 8.2, SAS Institute, Cary, NC, USA).

Where treatment–date interactions existed, multiple comparisons were performed to determine treatment differences within sampling dates, using the Bonferroni correction, α/n, to adjust for tests of significance. Multiple comparisons were also used to test *a priori* hypotheses that variables within treatments would differ (see Table 1): (i) before and after winter rainfall (30 November 2005 vs. 10 January 2006); (ii) before and after a winter dry down event (10 January vs. 6 February); (iii) before and after mid-spring rainfall (6 February vs. 8 March); (iv) before and after mowing of cover crops or tilling the 'Cultivation' treatment (tilling: 21 March vs. 13 April; mowing: 13 April vs. 26 April); (v) before and after late spring rainfall (9 May vs. 30 May); (vi) before and after fall rainfall (19 September vs. 10 October) (Bonferroni correction, 0.05/18 = p-value <0.003). While statistical analyses and tests of significance were performed on transformed variables in most cases (see above), all tables and graphs are presented with original data.

3. Results and discussion

3.1. Soil water content and temperature

GWC reflected precipitation events (Fig. 1), and typically, it did not differ by treatment except in spring. In early spring (8 March to 21 March), when precipitation frequency was high, soil water content was 1.25-fold greater in the cover crops than 'Cultivation' ($p < 0.05$) (Fig. 1; Table 2). This may be attributed to reduced runoff and increased infiltration in cover crop treatments (R. Smith, unpublished data). In late spring (26 April to 30 May), soil water content in both cover crops was 0.8-fold lower than 'Cultivation' ($p < 0.05$), just after cover crops reached peak biomass and were mowed, indicating that the

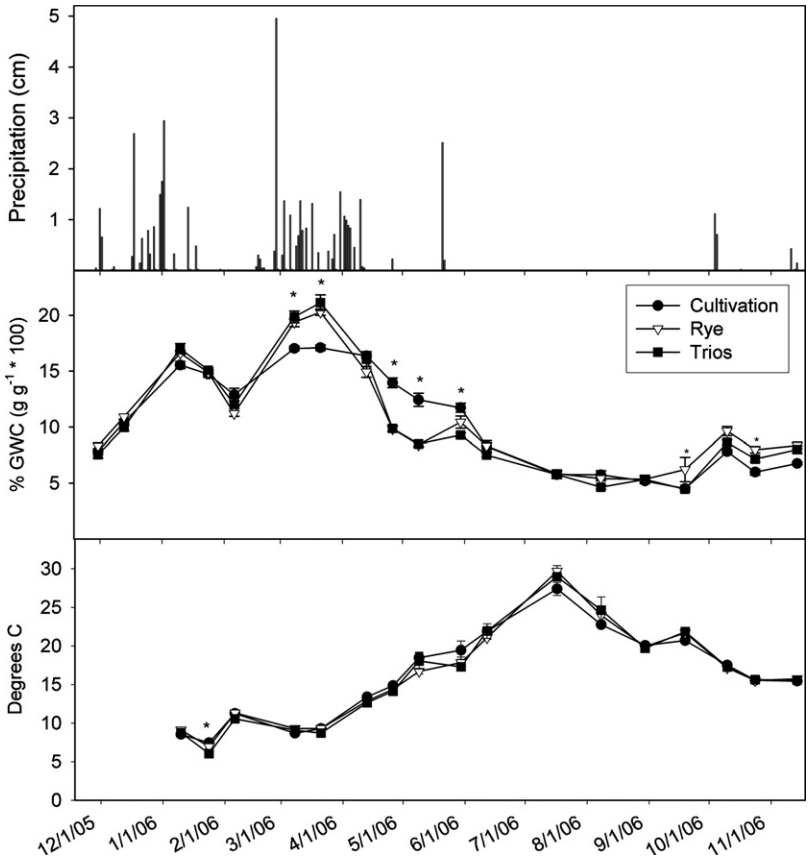

Fig. 1 – Annual precipitation and means and standard errors of gravimetric water content (GWC) and soil temperature by treatment ('Trios', 'Rye' and 'Cultivation'). Analysis of variance (mixed model) was used to determine significance of treatments, time, and time × treatment. Treatment legend corresponds to graphs of both GWC and soil temperature. Asterisks indicate that cover crop treatments are significantly different from 'Cultivation' on the given date as determined by multiple comparisons using the Bonferroni correction, α/n, to adjust for tests of significance (0.05/57 = p-value < 0.0009). Values for GWC and soil temperature are expressed on a per gram dry soil basis.

cover crop treatments may have experienced a period of high evaporative demand. When there was no precipitation in summer, soil water content was lowest, ranging from 5% to 8% among all treatments, and in late fall (October), soil water content increased in response to precipitation ($p < 0.05$). Soil temperature did not differ among treatments, and reflected typical seasonal patterns for a Mediterranean-like climate; there was an increase in soil temperature from winter to summer and then a subsequent decrease between summer and fall. It is likely that no difference in soil temperature was observed among treatments as the measurements are integrated across the length of the soil temperature probe associated with the LI-COR 6400, and shifts in soil temperature would have been less extreme below the soil surface (Hillel, 1982). Soil temperature generally followed an inverse pattern of soil water content, such that when soil water content increased, soil temperature decreased.

3.2. *Effects of plant biomass on SOM and labile C pools*

The two cover crops had contrasting growth patterns and effects on weed suppression. Little to no seedling emergence occurred until mid-December (ca. <1.0 g dry biomass m^{-2}). In late winter and early spring (i.e., 6 February and 8 March, respectively), aboveground plant biomass in 'Rye' was significantly greater than 'Trios' (Tables 2 and 3). However, these differences between cover crop treatments reversed prior to mowing in late spring (April). During the cover crop growth season, aboveground weed biomass was 30-fold (8 March), and ninefold (21 March) greater in 'Trios' than 'Rye', and 'Trios' tended to have greater weed biomass than 'Rye' on any given sampling date. This, in combination with the lack of differences in soil water content and inorganic N pools in 'Trios' and 'Rye' (Steenwerth and Belina, 2008), suggest that the greater aboveground cover crop biomass in 'Rye' may have depressed weed biomass growth through shading effects (Chauhan et al., 2006) (Fig. 1; Table 3). Also, by combining cover crop and weed biomass, ANPP was greater in 'Rye' than 'Trios' in winter (January to February), but in spring (March to May), it was greater in 'Trios' than 'Rye' ($p < 0.05$; data not shown).

After 5 years of cover cropping or cultivation, SOM showed distinct differences by treatment ($p < 0.05$). 'Trios' had 1.1-fold greater total soil C than 'Rye', and both cover crop treatments were 1.4-fold greater than 'Cultivation' (Table 4). The values for total soil C are within the range for agricultural soils found

Table 2 – F and p values for analysis of variance of biweekly variables

	Effect	Cover	Date	Cover × date
GWC[a]	F	1.2	339.24	8.11
	p	0.3895	<0.0001	<0.0001
MBC[a]	F	155.44	9.79	1.37
	p	0.0002	<0.0001	0.1269
$RESP_{mic}$[a]	F	357.03	9.79	3.03
	p	<0.0001	<0.0001	<0.0001
DOC[a]	F	128.99	16.99	1.63
	p	<0.0001	<0.0001	0.0463
CO_2 efflux[a]	F	8.25	7.89	2.77
	p	0.0191	<0.0001	0.0002
Cover crop biomass[a]	F	28.13	190.16	10.98
	p	0.0112	<0.0001	0.0008
Weed biomass[a]	F	337.64	6.1	2.63
	p	0.0029	0.0297	0.1449
Root biomass, 0–10 cm[b]	F	10.49	n.a.	n.a.
	p	0.0317	n.a.	n.a.
Root biomass, 10–20 cm[b]	F	1.05	n.a.	n.a.
	p	0.3638	n.a.	n.a.

n.a. indicates not applicable as root biomass was only sampled on one date.
[a] ANOVA conducted by mixed model.
[b] ANOVA conducted by general linear model.

Table 3 – Means and standard errors of cover crop and weed biomass

Date	Cover crop biomass ($g\ m^{-2}$)		Weed biomass ($g\ m^{-2}$)	
	Rye	Trios	Rye	Trios
10 January	12.87 ± 1.25a	8.49 ± 0.22a	<1.0[a]	<1.0
24 January	42.09 ± 2.40a	23.18 ± 2.01a	<1.0	<1.0
6 February	103.55 ± 7.85a	35.79 ± 1.96b	6.38 ± 3.46a	14.30 ± 7.06a
8 March	126.34 ± 9.45a	96.19 ± 7.42b	2.86 ± 1.02a	60.346 ± 24.06b
21 March	159.38 ± 16.83a	120.05 ± 24.15a	19.80 ± 4.92a	177.32 ± 70.91b
13 April	290.03 ± 46.92a	341.16 ± 52.54a	84.92 ± 37.68a	126.06 ± 48.70a

Letters indicate significant differences between treatments on a given day within biomass type at $p < 0.05$.
[a] Weeds occurred in small quantities (ca. <1.0 $g\ m^{-2}$) but were not present within randomly placed quadrats.

in this region (Steenwerth et al., 2002). No difference in total C in root and aboveground plant tissue was observed between cover crops. In spring, root biomass in the surface (0–10 cm) was 2.5-fold greater in 'Trios' than 'Rye', but no difference was observed in the lower layer (10–20 cm) (Tables 2 and 3).

Although these data represent just 1 year of cover crop growth, they lend some support to the hypothesis that 'Trios' increased soil C content relative to 'Rye'. The difference in soil C content between the cover crops may be partly attributed to these differences in ANPP, but root derived organic matter has

Table 4 – Means and standard errors of root biomass, root tissue C, aboveground tissue C, total soil C, and total annual CO_2 efflux by treatment[a]

Description	Units	n	'Cultivation'	'Rye'	'Trios'
Root biomass, 0–10 cm	$g\ m^{-2}$	3	n.d.	0.064 ± 0.029a	0.167 ± 0.011b
Root biomass, 10–20 cm	$g\ m^{-2}$	3	n.d.	0.006 ± 0.001a	0.004 ± 0.000a
Root, total C, 0–10 cm	$mg\ kg^{-1}$	3	n.d.	303.67 ± 26.30a	299.33 ± 7.33a
Root, total C, 10–20 cm	$mg\ kg^{-1}$	3	n.d.	333.33 ± 15.77a	334.00 ± 23.25a
Aboveground tissue C	$mg\ C\ kg^{-1}$	6	n.d.	431.7 ± 33.3	441.0 ± 32.1
Total soil C, 0–15 cm	$mg\ C\ kg^{-1}$	6	7.18 ± 0.18	9.45 ± 0.34	10.98 ± 0.30
Total annual CO_2 efflux	$g\ CO_2$–$C\ m^{-2}\ year^{-1}$	6	152.9 ± 10.8	267.8 ± 18.7	290.9 ± 16.0

n.d. indicate that it was not determined for the respective treatment. Letters indicate difference in treatment at $p < 0.05$ for the given variable.
[a] Root samples collected in March 2006; samples contain cover crop and weed roots.

been shown to be a greater contributor to SOM than C from aboveground plant biomass (Gale and Cambardella, 2000). Therefore, the greater total soil C content in 'Trios' than 'Rye' is more likely linked to greater root biomass, as well as rhizodeposition from root exudation and turnover (Shamoot et al., 1968; Hanson et al., 2001). These differences in soil C content and root biomass between 'Trios' and 'Rye' suggest that the individual cover crops may have distinct potentials for improving SOM content, at least in the soil surface. Although efforts were made to sample for cover crop roots away from weedy areas, greater weed biomass in 'Trios' than 'Rye' suggests that fine roots from weeds also contributed to these differences between cover crop treatments. Clearly, the presence of cover crops and the lower tillage frequency over the 5-year term of these treatments enhanced total soil C content. In support, SOM measured annually in these treatments from 2003 to 2005 increased over time in both cover crop treatments (R. Smith, unpublished data).

Cover crop soils also had greater labile C pools (MBC and DOC) and microbiological function, or $RESP_{mic}$, than 'Cultivation'. MBC in both 'Trios' and 'Rye' was consistently 2–4-fold greater than 'Cultivation', and there was a significant effect of sample date, such that MBC was greater during the winter and spring than summer, when soils had lower water content ($p < 0.05$; Table 2, Figs. 1 and 2). Following suit, cover crops consistently had 2–6-fold greater $RESP_{mic}$ than 'Cultivation', except on 6 February, when all treatments were significantly different from each other, and 19 September when only 'Trios' was significantly different from 'Cultivation'. Likewise, DOC was approximately 1.5–3-fold greater in cover crop treatments than 'Cultivation' on most dates.

The greater values of MBC, DOC, and $RESP_{mic}$ in 'Trios' and 'Rye' than 'Cultivation indicate that the presence of a cover crop and the absence of frequent tillage enhanced labile C pools, as has been observed in annual cropping systems in the same growing region (Fig. 2) (Jackson, 2000; Jackson et al., 2003, 2004). MBC of the vineyard cover crop treatments was approximately 50 $\mu g\ C\ g^{-1}$ greater than values measured in an annual agroecosystem that incorporated minimum tillage, compost additions, and a rotation of lettuce and cover crops (*S. cereale*) on more silty soils in the same growing region (Jackson et al., 2004), suggesting that lower tillage frequency

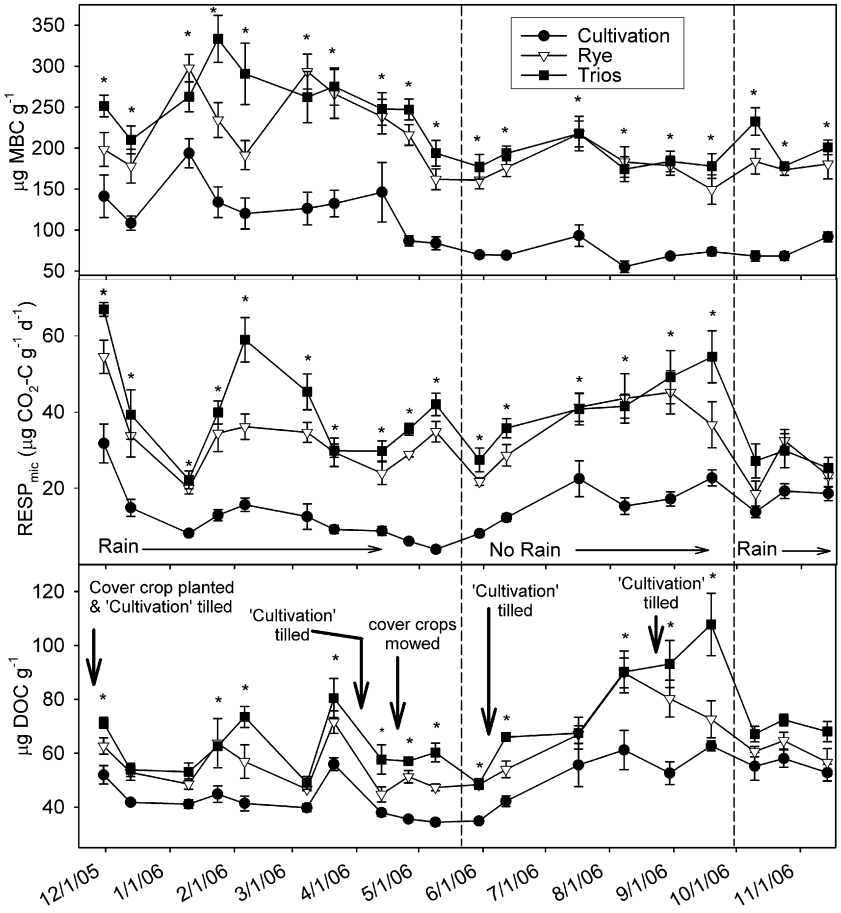

Fig. 2 – Means and standard errors of microbial biomass carbon (MBC), potential microbial respiration ($RESP_{mic}$), and dissolved organic carbon (DOC) by treatment ('Trios', 'Rye' and 'Cultivation'). Analysis of variance (mixed model) was used to determine significance of treatments, time, and time × treatment. Treatment legend corresponds to graphs of MBC, $RESP_{mic}$, and DOC. Asterisks indicate that treatments are significantly different from each other on the given date as determined by multiple comparisons using the Bonferroni correction, α/n, to adjust for tests of significance (0.05/57 = *p*-value < 0.0009). Arrows indicate time of management event. Dashed vertical lines demarcate periods of rainfall. Values are expressed on a per gram dry soil basis.

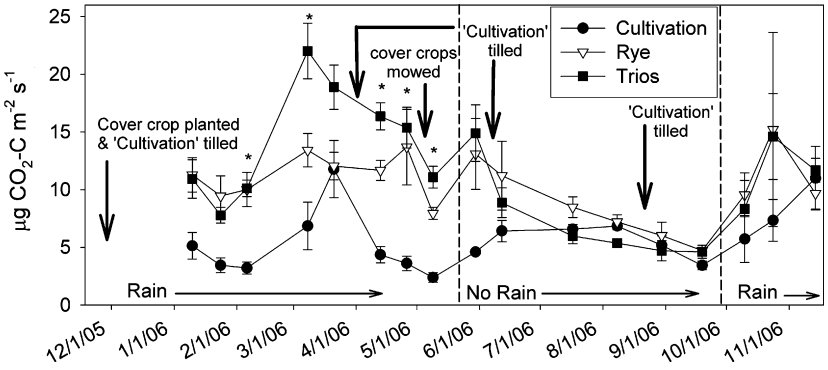

Fig. 3 – Means and standard errors of soil carbon dioxide (CO_2) efflux by treatment ('Trios', 'Rye' and 'Cultivation'). Analysis of variance (mixed model) was used to determine significance of treatments, time, and time × treatment. Asterisks indicate that treatments are significantly different from each other on the given date as determined by multiple comparisons using the Bonferroni correction, α/n, to adjust for tests of significance (0.05/51 = p-value < 0.001). Arrows indicate time of management event. Dashed vertical lines demarcate periods of rainfall. Values are expressed on a per gram dry soil basis.

in the vineyard increased MBC. Such increases in SOM, MBC and other labile C pools lead to benefits such as increased nutrient retention (e.g., immobilization of soil nitrogen), improved soil structure, infiltration and aeration, and enhanced ability of the soil to transfer excess nutrients (Barrett and Burke, 2000; Battany and Grismer, 2000). Indeed, the cover crop soils had a greater capacity for nitrogen mineralization, nitrification, denitrification, and greater microbial biomass nitrogen than the cultivated soils in this study (Steenwerth and Belina, 2008).

Table 5 – Multiple linear regressions of CO_2 efflux and MBC by treatment

CO_2 efflux[a]	'Cultivation'	'Rye'	'Trios'
GWC[b]	0.026	0.478[c]	0.597[c]
Soil temperature[b]	0.207	0.124	0.035
MBC[b]	0.409[c]	−0.013	−0.154
DOC[b]	0.327[c]	−0.210	0.240[c]
$RESP_{mic}$[b]	0.026	0.091	−0.039
Adj. r^2	0.183	0.212	0.452
p[d]	0.003	0.001	<0.0001
MBC[e]	**'Cultivation'**	**'Rye'**	**'Trios'**
GWC[b]	0.756[c]	0.873[c]	0.423[c]
Soil temperature[b]	−0.121	0.132	−0.330[c]
DOC[b]	−0.286[c]	0.020	0.102
$RESP_{mic}$[b]	0.681[c]	0.364[c]	0.307[c]
Adj. r^2	0.569	0.496	0.492
p	<0.0001	<0.0001	<0.0001

[a] Multiple linear regression of CO_2 efflux on gravimetric water content (GWC), soil temperature, microbial biomass carbon (MBC), dissolved organic carbon (DOC), and potential microbial respiration ($RESP_{mic}$).
[b] Standardized estimates, or beta coefficients, listed in columns indicate relative strength of each predictor for each treatment.
[c] Indicates predictor has a significant regression effect at $p < 0.05$.
[d] p-Value indicates significance of regression model by treatment.
[e] Multiple linear regression of MBC on GWC, soil temperature, DOC, and $RESP_{mic}$.

3.3. *Soil CO_2 efflux and management practice*

Both cover crops had consistently greater values in CO_2 efflux than 'Cultivation', except on 8 March and 13 April when only 'Trios' was significantly different from 'Cultivation' (Tables 1 and 2, Fig. 3). Discrete management events (i.e., mowing and tilling) displayed only minor effects on CO_2 efflux. For example, when 'Cultivation' was tilled in the spring, CO_2 efflux decreased threefold from the date prior to tillage ($p < 0.05$). The immediate increase in CO_2 efflux from tillage that has been attributed to physical release was not observed as measurements were collected approximately 1 week after tillage occurred (Reicosky et al., 1997; Calderón et al., 2000). Calderón et al. (2000) demonstrated that microbial respiration can decrease within days after tillage disturbance. In summer, there was no significant change in CO_2 efflux after tillage in 'Cultivation'. Although labile C pools were potentially available in all treatments as indicated by the increases in $RESP_{mic}$, lack of increase in CO_2 efflux from 'Cultivation' in response to tillage in summer is also partly attributed to low soil moisture, which has been linked to decreased magnitude of CO_2 efflux in response to tillage in spring wheat in Canada (Fig. 2) (Curtin et al., 2000).

Annually, total soil CO_2 efflux was greatest in 'Rye' and 'Trios' followed by 'Cultivation' (Table 4) ($p < 0.05$; data not shown). These annual emission rates are four to five times lower than annual CO_2 efflux measured in a vineyard in California's Napa Valley (Oakville, CA) (Carlisle et al., 2006). Contributing to the differences in annual CO_2 efflux between these two vineyards, annual precipitation in Oakville was approximately fourfold greater, soil organic C was two to threefold greater, and the soil was more finely textured (i.e., clay loam) than in Greenfield, the site of the current study.

3.4. *Relationships between labile C pools and season*

Significant multiple linear regressions of MBC on GWC, soil temperature, $RESP_{mic}$, and DOC occurred in all treatments (Table 5). In all cases, GWC was significant, positively correlated with MBC, and explained the most variation in

MBC, as indicated by its high standard estimates. In 'Cultivation' and 'Rye', GWC was followed by $RESP_{mic}$ in terms of explaining the variation in MBC. Soil temperature was only significant in 'Trios', and its standardized estimate was similar to $RESP_{mic}$. These results indicate that changes in MBC were strongly dependent on soil moisture and labile C pools in all treatments. Carbon pools derived from previous cover crops may have also contributed to the difference in MBC between cover crop treatments and 'Cultivation'. The absence of a significant treatment × date interaction for MBC suggests that the cover crop treatments sustained greater values in labile C pools, potential C availability (i.e., $RESP_{mic}$) and CO_2 efflux than 'Cultivation' not only from the current season's cover crop growth, but because soil microorganisms also utilized SOM derived from cover crops grown in previous years (Table 2; Figs. 2 and 3).

Concurrent changes in potential microbial respiration (i.e., $RESP_{mic}$), DOC, and CO_2 efflux were sensitive to shifts in soil water content (Tables 1 and 2; Figs. 1–3). In winter, when cover crop and weed growth was low and soil water content increased due to precipitation, $RESP_{mic}$ decreased in all treatments, which coincided with an increase in CO_2 efflux and a slight decrease in DOC over that same period ($p < 0.05$). In late winter, concurrent with increased cover crop growth, $RESP_{mic}$ increased in both cover crop treatments, but 'Trios' exhibited a 1.5-fold greater increase than 'Rye' ($p < 0.05$). In spring, the decreases in $RESP_{mic}$ and DOC corresponded to an increase in soil water content from precipitation (6 February to 21 March) ($p < 0.05$), suggesting that a portion of DOC had been available to soil microbes. After mowing, as DOC increased from summer to fall, both 'Trios' and 'Rye' had 1.5–3 times greater DOC than 'Cultivation' ($p < 0.05$), but did not differ from each other. This increase in DOC in 'Cultivation' can be partly attributed to the late season annual weeds (ca. 10% cover) that were tilled into the soil during weed control in spring and summer. Finally, in October, just after initial fall precipitation, which fell after a dry summer, DOC and $RESP_{mic}$ in both 'Trios' and 'Rye' decreased by approximately half the level present prior to fall rains ($p < 0.05$). This drop in $RESP_{mic}$ also was preceded by increased CO_2 efflux in the field from the cover crop treatments ($p < 0.05$).

These patterns in DOC, $RESP_{mic}$ and CO_2 efflux suggest that their responses were interrelated and influenced by changes in soil moisture content. Corresponding decreases in DOC and $RESP_{mic}$ and increases in CO_2 efflux suggest that these labile C pools served as C sources for CO_2 efflux and were respired with alleviation of low soil water content by precipitation, especially in fall when root respiration from cover crops and weeds was absent (Fierer and Schimel, 2002; Steenwerth et al., 2005). The CO_2 efflux that occurs after increases in soil water content has been linked to several factors. These include physical displacement of CO_2 (Reicosky et al., 1997), turnover of microbial cells due to increased stress with rewetting (Kieft et al., 1987; Lundquist et al., 1999a,b), increased availability of plant derived C with repeated wet–dry cycles, which are common in Mediterranean climates (van Gestel et al., 1993), and relief of soil water content limitations on microbial activity (Lundquist et al., 1999a). It is not possible to distinguish the relative contributions of root and microbial respiration to soil respiration, except in fall, when cover crops are absent, although even in the absence of the cover crops, root respiration from adjacent grapevines from late spring to early fall (April to October) likely added to total CO_2 efflux.

Observed decreases in DOC may also be caused by leaching below the sampled depth (0–15 cm), as has been observed in an annual cropping system in which cover crops were cultivated (Vinther et al., 2006). The increase in DOC and $RESP_{mic}$ over summer and the corresponding low CO_2 efflux across all treatments suggest that microbial utilization of DOC was limited by soil water content at that time (Lundquist et al., 1999a). Additionally, the summertime increase in DOC in all treatments may also be linked to the upward movement of DOC from soil water evaporation (Lundquist et al., 1999a) and MBC turnover, as indicated by the decrease in MBC (see Fig. 2).

3.5. *Potential drivers of vineyard CO_2 efflux*

Increases in CO_2 efflux were linked to increased soil water content from rainfall events and vineyard floor treatment (Figs. 1 and 3). On a given sampling date, soil CO_2 efflux was 2–3 times greater in the cover crop treatments than 'Cultivation' during winter and spring when soils were moist from precipitation ($p < 0.05$). In particular, CO_2 efflux in mid-spring increased in all treatments when soil water content was highest, but there was a lag in the increase in CO_2 efflux in 'Cultivation' compared to the cover crop treatments ($p < 0.05$). In summer, when soil water content was low, soil CO_2 efflux was similar among all treatments. In fall, soil CO_2 efflux increased in all treatments in response to the first rainfall ($p < 0.05$). No difference among treatments was detected due to great variability in the measurements after fall rains, though the cover crops tended to have greater CO_2 efflux than 'Cultivation'. Although not directly measured here, root respiration from both cover crops and grapevines likely contributed to soil CO_2 efflux (Hanson et al., 2001).

Soil temperature has long been utilized as a predictor of soil CO_2 efflux, but this relationship was not clearly exhibited in the current study. Among the variates GWC, soil temperature, MBC, $RESP_{mic}$, and DOC, few were significant in explaining patterns in CO_2 efflux using multiple linear regressions. In 'Trios', GWC and DOC were significantly correlated to CO_2 efflux, and GWC explained more variation than DOC as indicated by its higher standardized estimate value (Table 5). In 'Rye', only GWC was significant in explaining variation in biweekly measurements of CO_2 efflux. In 'Cultivation', MBC and DOC were significantly correlated to CO_2 efflux, and MBC explained more variation than DOC. The poor relationship between soil temperature and CO_2 efflux has been observed in other systems, including grasslands in Denmark (Eriksen and Jensen, 2001), and soybean and no-till corn in the Midwest region of the U.S. (Parkin and Kaspar, 2003). This discrepancy has been attributed to a 'lag effect', in which CO_2 efflux is more closely correlated with soil temperatures that were detected approximately 2–3 h previously, but whether this adequately explains the discrepancy of soil temperature and CO_2 efflux in these bimonthly measurements is unclear. Paul et al. (1999) also found a better correspondence between soil respiration rates and air temperature than soil temperature. Here, regression analysis tends to suggest that soil water content, not C availability (i.e.,

$RESP_{mic}$, DOC) or soil temperature, limited CO_2 efflux in the cover crop treatments. This hypothesis is further supported by the fact that $RESP_{mic}$ and DOC increased over the summer while CO_2 efflux did not. Similar relationships between soil respiration, temperature, and water content have been documented in a California vineyard (Carlisle et al., 2006), as well as Mediterranean forests and semiarid steppe in Spain and Italy (Casals et al., 2000; Rey et al., 2002; Maestre and Cortina, 2003). In contrast, the significant relationship between labile C pools and CO_2 efflux in 'Cultivation', with its lower labile C pools and total soil C, suggests that these factors may be more important in determining CO_2 efflux under relatively more C limiting conditions.

4. Conclusion

Carbon dioxide efflux and labile C pools responded to shifts in soil water content and cover crop presence. In this vineyard, both cover crop treatments were more effective at enhancing SOM content and sustaining higher potential microbial respiration and MBC than 'Cultivation'. Despite similar MBC, DOC, potential microbial respiration, annual CO_2 efflux and aboveground C content between the two cover crop treatments, greater ANPP in 'Trios' indicates that this cover crop treatment provided more soil C than 'Rye' during this study. However, annual differences in root turnover, exudation patterns, overall rooting depth and total belowground biomass could distinguish the overall soil C contributed by the respective cover crops. Weed establishment and growth also are both highly sensitive to annual growing conditions in vineyards (Baumgartner et al., 2007; Gago et al., 2007). Thus, ANPP in 'Trios' may not consistently occur at these levels as its greater ANPP was due in part to higher weed biomass. Nonetheless, this study demonstrates that SOM content, MBC, and microbiological function are augmented by growing cover crops in this vineyard, and that soil C dynamics and CO_2 efflux are highly sensitive to seasonal conditions, especially soil water content, in a Mediterranean climate.

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